

SENEGALIA BERLANDIERI, *S. CRASSIFOLIA*, AND *S. RENIFORMIS* HYBRIDS
(FABACEAE: MIMOSOIDEAE) IN CENTRAL AND NORTHERN MEXICO

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ABSTRACT

Principal component analyses (PCA) and principal coordinate analyses (PCoA) suggest that *Senegalia berlandieri* (Benth.) Britton & Rose hybridizes with *S. crassifolia* (A. Gray) Britton & Rose, the resulting hybrid being *S. × anisophylla* (S. Watson) Britton & Rose. This uncommon hybrid is reported from the states of Coahuila, Durango, and San Luis Potosí, Mexico. In addition, PCA and PCoA suggest that *S. berlandieri* hybridizes with *S. reniformis* (Benth.) Britton & Rose. The resulting hybrid, *S. berlandieri × reniformis*, also is infrequent, being restricted to the state of Querétaro, Mexico. The morphological features of both probable F₁-hybrids are highly variable. The backcrosses to each respective parent were also examined. The hybrid between *S. berlandieri* and *S. reniformis* (*Senegalia × zamudii* Seigler, Ebinger, & Glass) is described.

Key Words: Fabaceae, Mimosoideae, principal component analysis, *Senegalia*.

Among New World species of the genus *Senegalia*, which consists of 110 species in tropical and subtropical areas ranging from the southwestern United States south to Argentina (Seigler et al. 2006), hybrids are uncommon. Those hybrids that we have encountered in our monographic study of this genus mostly involve species apparently related to *S. berlandieri* (Benth.) Britton & Rose and are restricted to central and northern Mexico and the adjacent southwestern United States (Britton and Rose 1928; Turner 1959; Correll and Johnston 1970; Johnston 1975; Maslin and Stirton 1997; Glass and Seigler 2006; Seigler et al. 2006; Seigler et al. 2012). The present study was undertaken to examine the morphological differences and affinities of hybrids and hybrid populations involving *S. berlandieri* and the related species *S. crassifolia* (A. Gray) Britton & Rose and *S. reniformis* (Benth.) Britton & Rose in central and northern Mexico. We consider *Acacia sororia* Standl., Contr. U.S. Natl. Herb. 20:186. 1919 (= *Senegalia sororia* [Standl.] Britton & Rose, N. Amer. Fl. 23:108. 1928) to be a synonym of *S. reniformis*.

MATERIALS AND METHODS

Two separate analyses were conducted: one including *Senegalia berlandieri*, *S. crassifolia*, and their probable hybrid [*S. × anisophylla* (S. Watson) Britton & Rose]; and another including *S. berlandieri*, *S. reniformis*, and their apparent hybrid (*S. berlandieri × S. reniformis*). These

analyses were based on herbarium specimens of the putative parents and hybrids from central and northern Mexico (Appendix 1). Specimens of these species and their hybrids collected by the authors and from several herbaria were separated into groups based on overall morphological similarity, scored for 10 characters (Appendix 2), and the data analyzed by principal component analysis (PCA) and principal coordinate analysis (PCoA). Three or more measurements were made for each continuous character of each specimen and plotted to confirm that gaps in the data exist.

A PCA to identify groupings of the specimens examined was carried out. For these analyses, the data were first standardized and a correlation matrix, eigenvalues, and eigenvectors were calculated using NTSYS-pc version 2.1 (Rohlf 2000). Eigenvectors were scaled by the square root of λ . The axes were rotated and the resulting loading values graphically represented as both two- and three-dimensional plots (Figs. 1 and 2).

To carry out the PCoA, Gower's resemblance coefficients were calculated (Legendre and Legendre 1983; Podani 1999) with Program Gower6 (BASIC software for calculation of Gower's coefficients; made available by T. A. Dickinson, Royal Ontario Museum). The nature of each character was designated as binary, multistate, or quantitative descriptors, and all characters were weighted equally. The data matrix was transformed by the DCENTER algorithm using distances squared and eigenvectors and eigenvalues calculated with NTSYS-pc version 2.1 (Rohlf

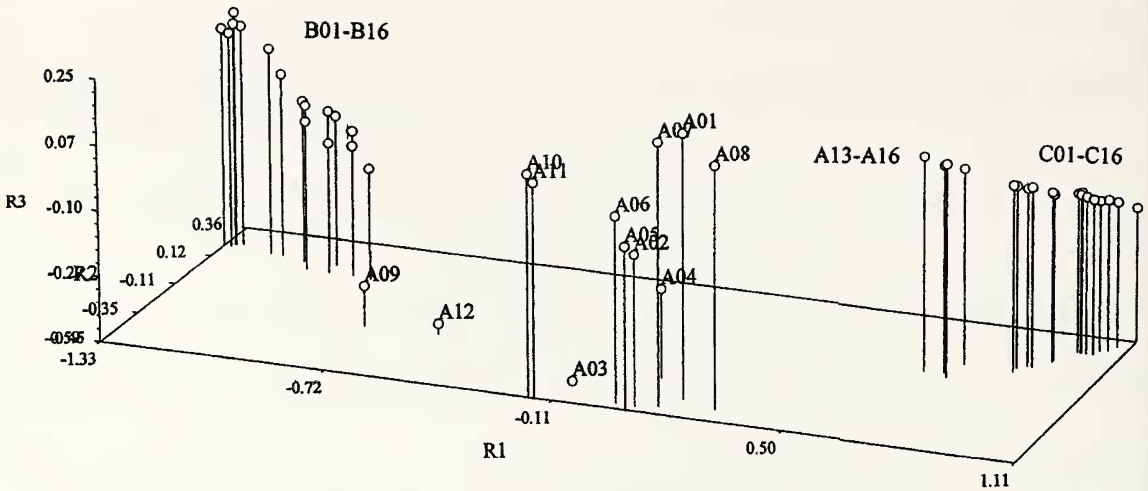


FIG. 1. Three-dimensional plot for the principal component analysis using 10 characters (Appendix 2) of 16 specimens of *Senegalia berlandieri* (B01-B16), 16 specimens of *S. crassifolia* (C01-C16), and 16 specimens of probable hybrids (*S.* × *anisophylla*) (A01-A16).

2000). Eigenvectors were scaled by the square root of λ . The resulting loading values were graphically represented as both two- and three-dimensional plots.

RESULTS

Senegalia berlandieri and *S. crassifolia*

A PCA and a PCoA based on Gower's similarity coefficients using 10 characters (Appendix 2) proved to be similar. Specimens of *S. berlandieri* (16), *S. crassifolia* (16), and *S.* × *anisophylla* (16) listed in Appendix 1 were used in these analyses. In the PCA, the first three principal components accounted for 96% of the

total variance. Leaflet pairs/pinna, pinna pairs/leaf, and leaflet length in mm (characters 5, 3, and 7) were most important for determining the component score of the first axis; leaflet shape, leaflet width in mm, and leaflet venation (characters 6, 8, and 9) were most important for determining the second axis. The species used in this analyses represented distinct groupings in both the PCA and PCoA. The results show that the parental species were well separated from each other, and that the putative hybrids were spatially located between the respective parental types. Putative backcrossed individuals to each of the parental species were positioned between each parental species and the probable F_1 -hybrids (Fig. 1).

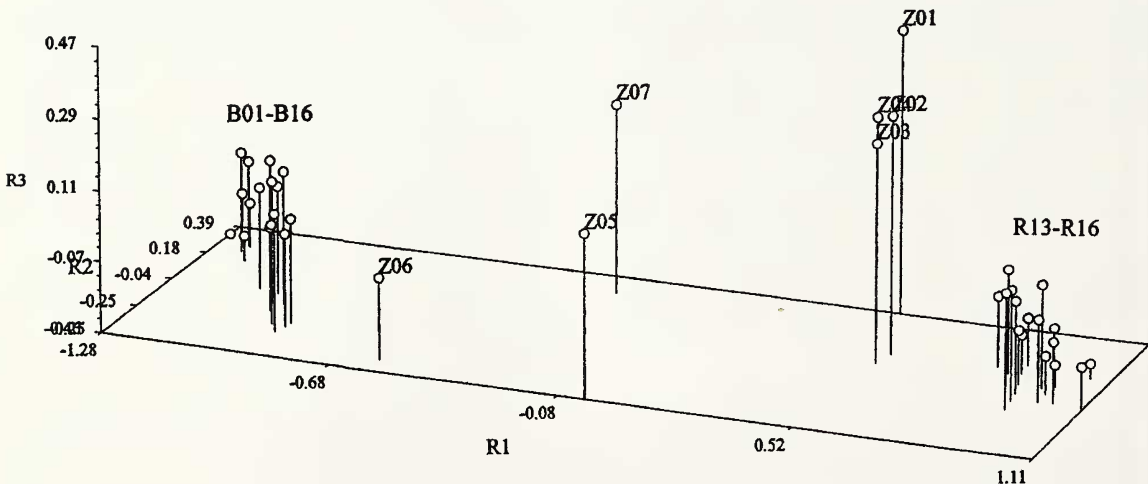


FIG. 2. Three-dimensional plot for the principal component analysis using 10 characters (Appendix 2) of 16 specimens of *Senegalia berlandieri* (B01-B16), 16 specimens of *S. reniformis* (R01-R16), and 7 specimens of probable hybrids (*S.* × *zamudii*) (Z01-Z06).

Senegalia berlandieri and *S. reniformis*

A PCA and a PCoA based on Gower's similarity coefficients proved to be similar. All specimens of *S. berlandieri* (16), *S. reniformis* (16), and *S. berlandieri* \times *reniformis* (7) listed in Appendix 1 were used in these analyses. In the PCA, the first three principal components accounted for 96% of the total variance. Leaflet length in mm, leaflet shape, and leaflet pairs/pinna (characters 7, 6, and 5) were most important for determining the component score of the first axis; leaf length in mm, pinna length in mm, and leaflet venation (characters 2, 4, and 9) were most important for determining the second axis. The species used in these analyses represented distinct groupings in both the PCA and PCoA. The results indicate that the parental species were well separated from each other and the F₁-hybrid spatially located between them. Apparent backcrossed individuals were present between each parental species and probable F₁-hybrids, respectively (Fig. 2).

DISCUSSION

Senegalia berlandieri and *S. crassifolia*

Of these taxa, *Senegalia berlandieri* has the most extensive distribution, occurring in south central and southern Texas, south into the states of Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Tamaulipas, and Zacatecas, Mexico. *Senegalia crassifolia*, in contrast, has a more restricted range, occurring in the states of Coahuila, Durango, San Luis Potosí, Tamaulipas, and Zacatecas, Mexico, and is considered to have a conservation status of "vulnerable" (Rico Arce 2007). The hybrid, *S.* \times *anisophylla*, is restricted to areas where the parental species overlap in distribution in Coahuila, Durango, San Luis Potosí, and Zacatecas, Mexico, and has been considered to have a conservation status of "vulnerable" (Rico Arce and Griffiths 2002) although recognized as a hybrid between *S. berlandieri* and *S. crassifolia* (Johnston 1975).

Senegalia \times *anisophylla* can easily be separated from both *S. berlandieri* and *S. crassifolia* using some of the characteristics listed in Appendix 2. The most obvious and commonly used characteristics include: leaves with 1 pinna pair in *S. crassifolia*, 2–4 pairs in *S.* \times *anisophylla*, and 7–19 pairs in *S. berlandieri*; and leaflets 1–rarely 2 pairs/pinna in *S. crassifolia*, 5–9 pairs/pinna in *S.* \times *anisophylla*, and 30 or more pairs in *S. berlandieri*. Occasional backcrossed individuals that are somewhat more difficult to identify were encountered. Two specimens (A09, A12) probably represent backcrosses of *S.* \times *anisophylla* to *S. berlandieri* (Fig. 1). Backcrosses of this type

differ from the F₁-hybrid in that they have 5–7 pinna pairs per leaf, 12–25 leaflet pairs per pinna, and oblong leaflets. Apparent backcrosses between *S.* \times *anisophylla* and the other parental type, *S. crassifolia* (A13, A14, A15, A16), differ from the F₁-hybrid by having 2–3 pinna pairs per leaf, 2–4 leaflet pairs per pinna, and large oval, orbicular, to obovate leaflets, some exceeding 25 mm in length. *Senegalia crassifolia* specimens, in contrast, have leaves with 1 pinna pair and usually 1 pair of leaflets/pinna.

Senegalia berlandieri and *S. reniformis*

Senegalia reniformis has a quite restricted range; we have only seen specimens from the states of Hidalgo and Querétaro, Mexico (Glass and Seigler 2006). The hybrid, *S. berlandieri* \times *S. reniformis*, has only been found in the state of Querétaro, Mexico, where the authors have collected specimens of the hybrid in locations where one or both parents were present in the same area.

Senegalia berlandieri \times *S. reniformis* is easily separated from both *S. berlandieri* and *S. reniformis*. The most obvious characteristic is that there are 1 or rarely 2 pairs of leaflets/pinna in *S. reniformis*, 3–16 pairs/pinna in the hybrid, and 30 or more pairs in *S. berlandieri*. Although useful for recognition when available, inflorescence structure was not used in the analyses as few specimens were in flower. *Senegalia berlandieri* has globose inflorescences, and *S. reniformis* has spicate inflorescences, whereas those of the hybrid are short spicate and less than twice as long as wide. Most specimens of *S.* \times *zamudii* Seigler, Ebinger, & Glass were collected from areas where *S. berlandieri* and *S. reniformis* occur sympatrically. In Figure 2, two specimens (Z05, Z07) probably represent F₁-hybrids. These specimens have oblong leaflets that average 10 mm in length with 4–10 leaflet pairs/pinna. Occasionally, apparent backcrossed individuals are encountered. Specimen Z06 between the F₁-hybrid and *S. berlandieri* has smaller leaflets that are similar to those of *S. berlandieri* and up to 15 pairs of leaflets/pinna. Apparent backcrosses between the F₁-hybrid and *S. reniformis* (Z01, Z02, Z03, Z04) differ from the F₁-hybrid by having 3–4 leaflet pairs per pinna, and large oval, orbicular, to obovate leaflets, some leaflets exceeding 15 mm in length (Fig. 2). *Senegalia reniformis* specimens, in contrast, have leaves with 1–2 pairs of leaflets/pinna. Based on these specimens, a proposed new hybrid is described. This hybrid is named after Dr. Sergio Zamudio Ruiz (Instituto de Biología, Facultad de Ciencias, Universidad Nacional Autónoma de México, presently at the Centro Regional del Bajío, Instituto de Ecología, Pátzcuaro, Michoacán), who has collected specimens of this new species and published extensively on the flora of this area of Mexico.

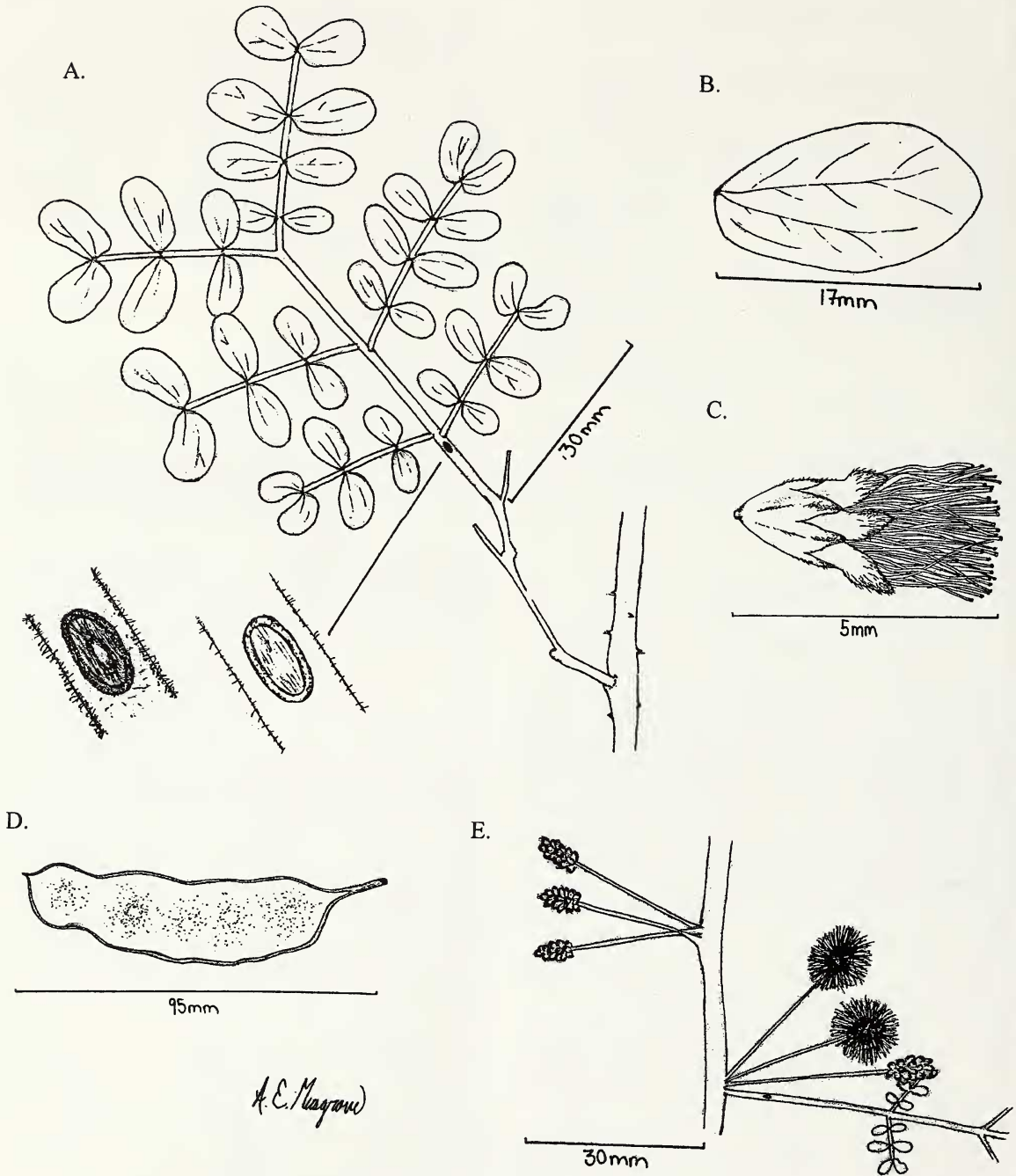


FIG. 3. *Senegalia zamudii* Seigler, Ebinger & Glass, A: Leaf with petiolar glands (*S. Zamudio* 247858). B: Leaflet (adaxial surface) (*S. Zamudio* 247858). C: Flower (*S. Zamudio* 994930). D: Fruit (*S. Zamudio* 247858). E: Clustered inflorescences with associated leaves and prickles (*S. Zamudio* 247858).

TAXONOMIC TREATMENT

Senegalia × *zamudii* Seigler, Ebinger, & Glass, nothomorph nov. (Fig. 3).—TYPE: MEXICO, Querétaro, Cañón del Río Extorax entre El Platano y El Timbre, alt. 900 m, 12 Dec 1999, *S. Zamudio*, *E. Esparza* & *E. Zamudio* 11241 (holotype: MEXU, photo ILL).

Senegalia × *zamudii* Seigler, Ebinger & Glass differs from other *Senegalia* species by shrubby habit, leaf size (40–90 mm), oval to reniform stipules, a solitary orbicular petiolar gland (0.8–2.5 mm long) usually located between the leaflets of the lowermost pinna pair, 2 to 6 pairs of pinnae per leaf, 3 to 16 pairs of leaflets per pinna, inflorescence a spike 10–20 mm long, peduncles

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- , ———, AND J. T. MILLER. 2006. The genus *Senegalia* (Fabaceae: Mimosoideae) from the New World. *Phytologia* 88:38–93.
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- APPENDIX 1
- SPECIMENS USED IN SCORED PRINCIPAL COMPONENT (PCA) AND PRINCIPAL COORDINATE (PCoA) ANALYSES
- Senegalia* × *anisophylla*: MEXICO. COAHUILA: 11 km N of Ahuichila, Cañón de Ahuichila, alt. 1250–1500 m, 15 Jun 1972, F. Chiang, T. L. Wendt & M. C. Johnston 7812 (NY); Sierra de Jimulco, 3 km N of Mina San José, 8 km NE of Estación Otto, alt. 1800–3138 m, 27 Sep 1972, F. Chiang, T. L. Wendt & M. C. Johnston 9539 (NY); Sierra de Jimulco, 3 km N of Mina San José, 8 km NE of Estación Otto, alt. 1800–3138 m, 27 Sep 1972, F. Chiang, T. L. Wendt & M. C. Johnston 9539a (NY); 5 km SW of La Rosita (San Miguel el Alto), alt. 1300 m, 29 Jun 1973, M. C. Johnston, T. L. Wendt & F. Chiang C. 11510 (MO); 5 km SW of La Rosita (San Miguel el Alto), alt. 1300 m, 29 Jun 1973, M. C. Johnston, T. L. Wendt & F. Chiang C. 11511 (MO); Mountains, cañones near Jimulco, 14 May 1885, C. G. Pringle 163 (NY); Sierra de Parras en el Ejido Chupaderos, alt. 1500 m, 28 May 1981, A. Rodríguez & M. A. Carranza s.n. (MU). DURANGO: 8 mi N of Cuencamé, 27 Jun 1977, J. D. Dwyer 14253A (MO); Estación Microndas "Sapioris," about 30 km SW of Gómez Palacio on road toward Durango, alt. 1400–1500 m, 25 Mar 1973, M. C. Johnston, T. L. Wendt & F. Chiang C. 10397 (MO); Estación Microndas "Sapioris," about 30 km SW of Gómez Palacio on road toward Durango, alt. 1400–1500 m, 25 Mar 1973, M. C. Johnston, T. L. Wendt & F. Chiang C. 10398 (MO); just S and SE of Estación Microondas "Sapioris," about 20 km NW of Estación Chocolate, alt. 1450–1500 m, 13–14 Aug 1973, M. C. Johnston, T. L. Wendt & F. Chiang C. 12200 (MO). SAN LUIS POTOSÍ: Dirt road to Los Anoles near border of Tamaulipas, 9 km S of El Huisache, alt. 1450 m, 3 Jun 1997, C. Glass & G. Glass 428 (ILL); dirt road to Los Anoles near border of Tamaulipas, 9 km S of El Huisache, alt. 1450 m, 3 Jun 1997, C. Glass & G. Glass 430 (ILL); 2 km SE of Huizache junction and about 5 km WSW of El Huizache, alt. 1400 m, 19 May 1973, M. C. Johnston, T. L. Wendt & F. Chiang C. 11119 (MO); 2 km airline SE of Huizache Junction, alt. 1400 m, 19 May 1973, M. C. Johnston, T. L. Wendt & F. Chiang C. 11120 (MO); E de Núñez, km 84 carretera San Luis-A. Morelos, alt. 1600 m, J. Rzedowski 5548 (F).
- Senegalia berlandieri*: MEXICO. COAHUILA: Sierra Mojada Mountains, 20 Apr 1892, M. E. Jones 195 (DS); Jimulco, 9 Apr 1886, C. G. Pringle 867 (MIN); Ejido el Capulín, 10 km al SW de Parras de la Fte. Mpio. Parras, alt. 2050 m, 6 Mar 1983, A. Rodríguez, M. A. Carranza & A. Orta 81 (ILL). GUANAJUATO: 10 km al SE de Xichú, alt. 1000 m, 4 Feb 1997, E. Pérez & S. Zamudio 3561 (MEXU). NUEVO LEÓN: Road to Galeana from Linares, alt. 630 m, 4 Jun 1997, C. Glass & G. Glass 435 (ILL). QUERÉTARO: El Platano, alt. 1000 m, 30 Nov 1992, R. Fernández N. 4839 (ASU); El Carnicero, alt. 1380 m, E. González 1439 (MEXU); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, D. S. Seigler, B. R. Maslin & C. Céspedes 16066 (ILL). SAN LUIS POTOSÍ: 17 km W of Tamuín, 21 Dec 1990, D. S. Seigler, J. E. Ebinger, H. Clarke & C. Gratton 13226 (ILL). TAMAULIPAS: Rancho Las Águilas, Carretera Soto la Marina–Aldama, 10 Mar 1992, J. L. Mora-López 141 (MEXU); Victoria, alt. 320 m, 1 Feb–9 Apr 1907, E. J. Palmer 30 (F); vicinity of Victoria, alt. 320 m, 1 Feb–9 Apr 1907, E. J. Palmer 124 (MO); 4.5 mi SW of Ciudad Victoria along road to Jaumave, alt. 1450 ft., 6 Apr 1955, I. L. Wiggins 13355 (SD). UNITED STATES. TEXAS. Hidalgo Co: Santa Ana National Wildlife Refuge, 14 Apr 1977, J. C. Solomon 2746 (MO). Val Verde Co.: 5 mi W of Langtry, 13 Apr 1963, A. C. Koelling 837 (ILL); 3 mi W of Langtry, 1 Apr 1954, O. E. Sperry 2970 (ILL).
- Senegalia crassifolia*: MEXICO. COAHUILA: 30 km al poniente de Parras, brecha Parras-Viesca, Dec 1993, M. A. Carranza, J. Luna & S. Comparán 2006 (TEX); 12 km N of Ahuichila, Cañón de Ahuichila, alt. 1300 m, 15 Jun 1972, F. Chiang, T. L. Wendt & M. C. Johnston 7808 (MO); NE edge of Cerro Bola, alt. 1150 m, 6 Jul 1972, F. Chiang, T. L. Wendt & M. C. Johnston 8286 (MO); Sierra de Jimulco and up to 3 km N of Mina San Jose, alt. 1800–3138 m, 27 Sep 1972, F. Chiang, T. L. Wendt & M. C. Johnston 9538 (MO); 18 km S de Parras de la Fuente, alt. 1400 m, 16 Sep 1982, A. Orta, M. A. Carranza, and A. Rodríguez 64 (TEX); Torreón, 13–20 Oct 1898, E. J. Palmer 474 (MO); hills near Jimulco, Apr–May 1885, C. G. Pringle 49 (WIS); Hwy. 40 at roads to San Pedro and Matamoros, 14 Jul 1975, D. S. Seigler & G. Holstein 9233 (ILL); 37 mi W of Paila on Hwy. 40, 28 May 1983, D. S. Seigler, J. Kramer & E. Carreira 12014 (ILL); mountain pass of La Peña, Nov 1852, G. Thurber 829 (MO). DURANGO: Estación Microndas "Sapioris" about 30 km SW of Gómez Palacio on hwy. toward Durango, alt. 1400–1500 m, 25 Mar 1973, M. C. Johnston, T. L. Wendt & F. Chiang

10406 (MO); 5.1 mi S of El Refugio, alt. 4000 ft, 21 Jul 1977, *E. Lehto, D. J. Pinkava, B. Parfitt & T. Reeves 21670* (NY). SAN LUIS POTOSÍ: 3 mi SE of Presa de Guadalupe, 1250 m, 24 Nov 1962, *R. Moran 10019* (SD); 1 km E de El Huizache, alt. 1310 m, 22 Jul 1983, *L. Rico & J. L. Contreras s.n.* (CM). TAMAULIPAS: SW of Tula, alt. 4400 ft, 26 Nov 1966, *H. D. Ripley & R. C. Barneby 14770* (NY). ZACATECAS: Sierra del Yeso, almost due W of La Presa de los Angeles, alt. 1400–1500 m, 30 Jun 1973, *M. C. Johnston, T. L. Wendt & F. Chiang C. 11532* (MO).

Senegalia reniformis: MEXICO. QUERÉTARO: Hwy. 120, S of Jalpán, 1 km E of Peñamiller, alt. 1160 m, 23 May 1997, *C. E. Glass, G. Glass, J. T. Carreón & J. Ramírez 382* (ILL); rocky north facing slope N of Cerro Gordo, alt. 1860 m, 23 May 1997, *C. E. Glass, G. Glass, J. T. Carreón & J. Ramírez 387* (EIU, ILL); rocky north facing slope N of Cerro Gordo, alt. 1860 m, 23 May 1997, *C. E. Glass, G. Glass, J. T. Carreón & J. Ramírez 389* (EIU, ILL); Hwy. 120 N of Higuerillas, km marker 92, *C. Glass, G. Glass, J. T. Carreón & J. O. B. Ramírez 397* (ILL); 7 km S of Peña Blanca on Hwy. 120, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15861* (EIU, ILL); 6 km N of jct. Hwy 120 to Jalpán and road to Peñamiller, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15862* (EIU, ILL); 6 km N of jct. Hwy 120 to Jalpán and road to Peñamiller, 29 Jan 2004, *D. S. Seigler, C. Céspedes & J. Seigler 15864A* (ILL); N of jct. of road to Peñamiller on Mexico Hwy. 120, the road to Jalpán, 3 Jun 1991, *D. S. Seigler, J. Ebinger, H. Clarke & K. Read 13669* (EIU, ILL); 4 km N of jct. of road to Peñamiller on Hwy. 120, the road to Jalpán, *D. S. Seigler, J. Ebinger, H. Clarke & K. Read 13675* (EIU, ILL); 4 mi N jct. of road to Peñamiller on Hwy. 120, road to Jalpán, 3 Jun 1991, *D. S. Seigler, J. Ebinger, H. Clarke & K. Read 13676* (EIU, ILL); 20 mi N of Vizarrón on Hwy. 120, 10 June

2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16064* (ILL); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16067* (ILL); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16068* (ILL); below lookout on road to Jalpán (second pull-off), 10 Jun 2005, *D. S. Seigler, B. R. Maslin & C. Céspedes 16069* (ILL); 6–7 km al S de Tolimán, 16 May 1978, *S. Zamudio R. 713* (MEXU); 1 km al N de Peñamiller, alt. 1515 m, 25 May 1977, *S. Zamudio R. 2094* (MEXU).

Senegalia × *zamudii*: Specimens listed under specimens examined after the description of *S.* × *zamudii*.

APPENDIX 2

CHARACTERS SCORED FOR THE PRINCIPAL COMPONENT ANALYSES (PCA) AND PRINCIPAL COORDINATE ANALYSES (PCOA) OF THE *SENEGALIA BERLANDIERII*/*S. CRASSIFOLIA* COMPLEX, AND THE *S. BERLANDIERII*/*S. RENIFORMIS* COMPLEX

1. Petiole gland position (Glp) 1 = near middle of petiole, 2 = base of first pinna pair.
2. Leaf length in mm (Lfl).
3. Pinna pairs/leaf (Pip).
4. Pinna length in mm (Pil).
5. Leaflets pairs/pinna (Len) 1 = 30–55, 2 = 3–29, 3 = 1–2.
6. Leaflet shape (Les) 1 = linear to oblong, 2 = obovate, oblanceolate to reniform.
7. Leaflet length in mm (Lel).
8. Leaflet width in mm (Lew).
9. Leaflet venation (Lev) 1 = not obvious, 2 = obvious.
10. Venation arrangement (Ven) 1 = pinnate, 2 = palmate.